

MORPHOTYPE VARIATION OF ORTHOPHRAGMINIDS AS A PALAEOECOLOGICAL INDICATOR: A CASE STUDY OF BARTONIAN LIMESTONES, POD CAPKAMI QUARRY, TATRA MTS, POLAND

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Abstract: *Nummulites-Discocyclus* bioclastic packstone and *Discocyclus* rudstone occur in the transgressive sequence of the Middle–Upper Eocene deposits in the Tatra Mts. The succession of the studied facies is a direct response to a rapid environmental change, related to progressive deepening. Facies transition from *Nummulites-Discocyclus* bioclastic packstone of proximal mid-ramp to *Discocyclus* rudstone of distal mid- and outer-ramp is an exemplary record of a deposition during deepening conditions. Increasing of diversity of the genus *Discocyclus*, decreasing of diversity of other foraminifera up the section and vertical variation of orthophragminid morphotypes from the ovate- through saddle- to the disc-shaped tests are related to deepening and shadowing of the depositional environment.

Key words: Larger benthic foraminifera, orthophragminids, morphotype, transgression, palaeoenvironment, Eocene, Tatra Mts, Western Carpathians.

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INTRODUCTION

The symbiont-bearing larger benthic foraminifera (LBF) are a good indicator of oligotrophic, tropical shallow marine carbonate depositional conditions, especially in terms of their environmentally sensitive depth distribution and morphology. An analysis of the morphology of larger foraminiferal tests provides a good tool for palaeoenvironmental reconstructions (e.g., Reiss & Hottinger, 1984; Hallock & Glenn, 1986; Hottinger, 1997; Hallock, 1999; Geel, 2000; Hohenegger, 2004, 2005, 2009). The distribution patterns of recent LBF were investigated as the environmental indicators in respect to depth, light limitations, type of substrate and energy regime (Hohenegger & Yordanova, 2001; Beavington-Penney & Racey, 2004; Jorriy *et al.*, 2006). Distribution of the recent LBF is strongly influenced by light level and by water energy (e.g., Larsen, 1976; Larsen & Drooger, 1977; Hallock *et al.*, 1986; Hallock, 1979, 1985; Hohenegger, 2009; Hallock & Pomar, 2008). The former factor strongly affects symbiont bearing LBF and determinates the shapes of LBF tests.

Orthophragminids (including genera *Discocyclus*, *Nemkovella*, *Orbitoclypeus* and *Asterocyclina* – *sensu* Less, 1987) extinct at the Eocene/Oligocene boundary and they have no present-day representatives. However, *Discocy-*

clina can be regarded as homeomorphs to recent *Cycloclypeus* (Hohenegger & Yordanova, 2001), whose habitat and environmental requirements are well known.

Knowledge on the palaeoecology of orthophragminids refers mainly to their morphology, palaeobathymetric distribution and faunal associations (Fermont, 1982; Ferrandez-Cañadell & Serra-Kiel, 1992; Ferrandez-Cañadell, 1998). According to Fermont (1982), the tests of *Asterocyclina* and *Discocyclus* become more flattened with increasing depth. *Discocyclus* test morphology is strongly environmentally influenced, mainly due to adaptation of the foraminifera to endosymbiotic algae (Ferrandez-Cañadell, 1998).

LBF are characteristic features of Eocene carbonate deposits in the Tatra Mts (Bieda, 1963; Olempska, 1973; Kulka, 1985). *Nummulites*, that are widely known as a palaeoenvironmental indicator (Beavington-Penney & Racey, 2004; Beavington-Penney *et al.*, 2006), constitute the most characteristic components of these deposits. Nonetheless, *Discocyclus* are dominant component in some facies of these deposits. They may be also a very important and useful tool for palaeoenvironmental reconstructions of Eocene deposits (e.g., Čosović *et al.*, 2004; Bassi, 2005; Nebelsick *et al.*, 2005).

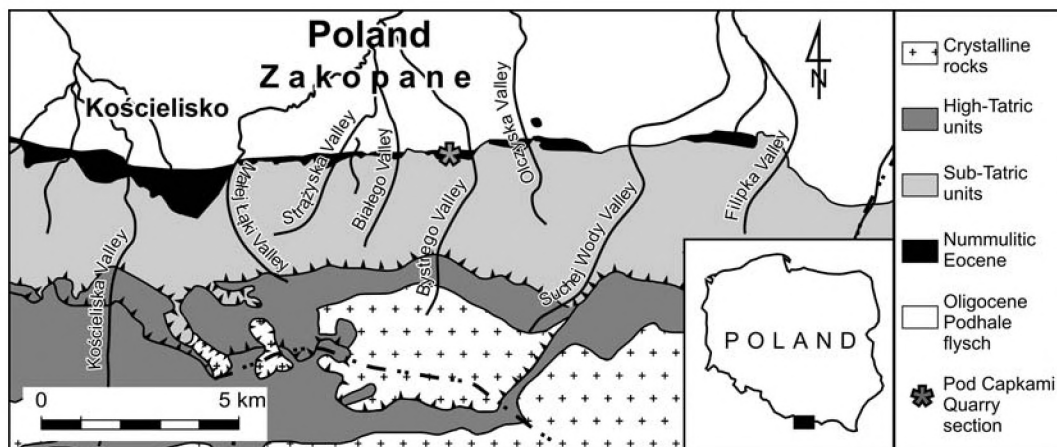


Fig. 1. Geological sketch map of the Polish part of the Tatra Mts (after Bac-Moszaszwili *et al.*, 1997, simplified)

A few examples of application of *Discocyclus* test morphology as a palaeoenvironment indicator are known (Ćosović & Drobne, 1995; Geel, 2000; Jach *et al.*, in press). The purpose of the study is the application of changes of orthophragminid morphology, diversity and abundance in the assemblage of LBF as palaeoenvironmental indicators.

GEOLOGICAL SETTING

The shallow water Eocene deposits are part of the so-called Central Carpathian Palaeogene complex (Passendorfer, 1959). The Middle–Upper Eocene deposits crop out along the northern margin of the Tatra Mts (southern Poland; Fig. 1). Generally, these deposits illustrate progressive deepening of depositional environment (Roniewicz, 1969; Kulka, 1985; Olszewska & Wiczeorek, 1998; Bartholdy *et al.*, 1999). The Eocene sequence commences with conglomerates composed of bedrock clasts (Fig. 2), covered by littoral extraclastic packstone with *Nummulites brogniarti* D’Archiac et Haime, which is locally capped by nummulitic bank facies with *Nummulites perforatus* (Montfort) of the Early Bartonian SBZ 17 (shallow benthic zone according to Serra-Kiel *et al.*, 1998). These deposits are, in turn, covered by *Discocyclus*-bearing facies comprising *Nummulites-Discocyclus* bioclastic packstone with *Nummulites perforatus* (Montfort), *Nummulites puschi* D’Archiac, of the Early Bartonian SBZ 17 zone, and *Discocyclus* rudstone containing in the uppermost part *Discocyclus augustae* Van der Weijden and *Operculina* aff. *alpina* Douville of the Late Bartonian SBZ 18. The rudstone is overlain by glauconitic marls with globigerinids (Alexandrowicz & Geroch, 1963; Olszewska & Wiczeorek, 1998; Olszewska, 2009). The uppermost part of the section is formed by organodetritic limestones and conglomerates. These deposits represent Priabonian SBZ 19 zone on the basis of *Operculina alpina* Douville, *Heterostegina reticulata* Rüttimeyer and *Nummulites fabianii* (Prever). The carbonates are succeeded by an about 2.5 km thick complex of Oligocene turbiditic deposits (Radomski, 1959).

Discocyclus-bearing facies, especially the transition from the *Nummulites-Discocyclus* bioclastic packstone to

Discocyclus rudstone, is a record of an abrupt transgression (Fig. 2). *Discocyclus*-bearing facies (*Nummulites-Discocyclus* bioclastic packstone and *Discocyclus* rudstone) occurs at several localities, such as the Strążyska Valley, Spadowiec Valley, Pod Capkami Quarry, Olczyska Valley, Jaszczurówka, and the Chłabówka Stream in the Tatra Mts (Fig. 1). The most representative, complete and relatively well documented section crops out in an abandoned Pod Capkami Quarry (Fig. 1; Bieda, 1963; Alexandrowicz & Geroch, 1963; see also Bartholdy *et al.*, 1995, 1999). This section was selected for detailed analysis (GPS coordinates: N49°16.746', E19°58.361').

MATERIAL AND METHODS

The studied Pod Capkami Quarry section contains *Discocyclus*-bearing facies, which crops out on the northern slope of Mała Krokiew (Fig. 1). The section was analysed bed-by-bed with detailed sampling. Polished slabs and thin sections were prepared for microfacies and palaeoecological analysis.

Since most of the *Nummulites-Discocyclus* bioclastic packstone samples have been collected from hard limestones, the microfacies and microfauna were studied mainly in thin sections. Samples of relatively poorly cemented *Discocyclus* rudstone were disaggregated and washed in order to extract the LBF tests, especially for identification of *Discocyclus* species (*sensu* Neumann, 1958). Specimens of foraminifera were picked from the residue and polished or split to obtain equatorial sections of the tests.

Biometric analysis of LBF is based on the thickness to diameter (T/D) ratio. The LBF were determined from axial or nearly axial sections, and orthophragminid from *Discocyclus* rudstone additionally were determined from isolated forms. A ratio of small megalospheric A-forms to large microspherical B-forms was identified only when equatorial sections were possible to be observed, that is on the basis of tests isolated from the *Discocyclus* rudstone.

Samples and thin sections are housed at the Institute of Geological Sciences of the Jagiellonian University.

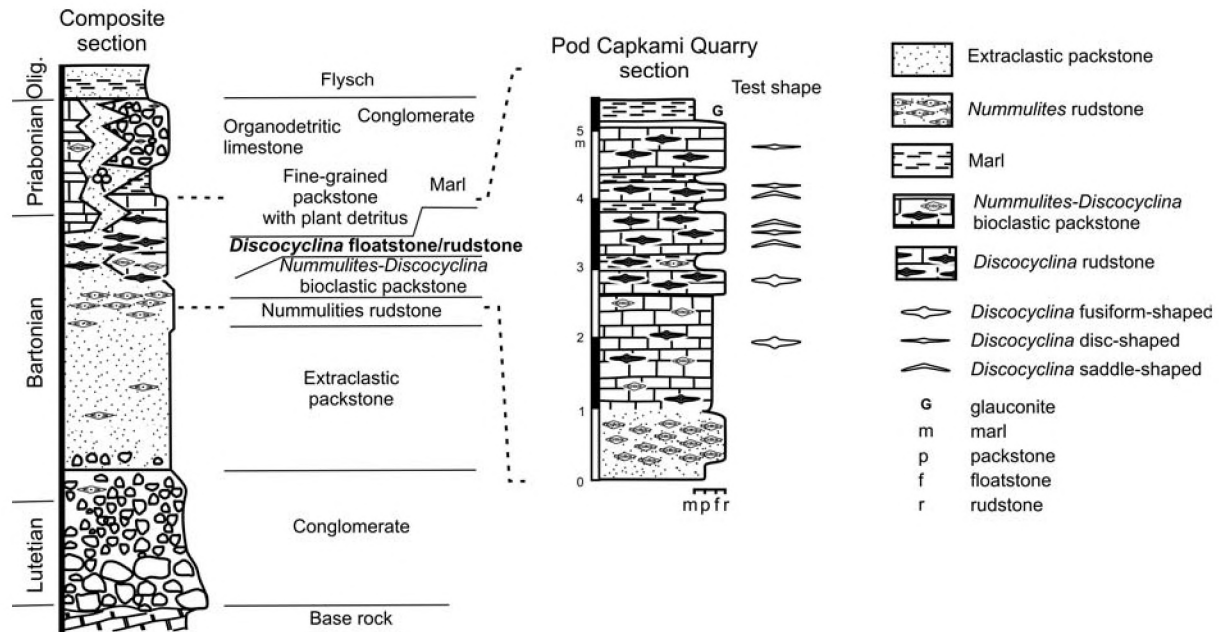


Fig. 2. Synthetic section of Eocene deposits in the Tatra Mts – left column. Right column – detailed section of the studied deposits in the Pod Capkami Quarry

RESULTS

Discocyclina-bearing facies comprises *Nummulites-Discocyclina* bioclastic packstone covered by *Discocyclina* rudstone. The *Nummulites-Discocyclina* bioclastic packstone, up to 1.5 m thick, is distinctly bedded (Figs 2, 3A). It is composed of numerous small *Nummulites* sp., spherical in axial section, accompanied by ovate or fusiform-shaped orthophragminids – representatives of *Orbitoclypeus* sp. and *Asterocyclina* sp., saddle-shaped *Discocyclina* sp., robust and spherical tests of *Nummulites perforatus* (Montfort), as well as flat disc-shaped *Nummulites* cf. *maximus* (Archiac), with maximum diameter up to 11 cm (Fig. 3B), and diversified roataliids, such as: *Asterigerina* sp. and *Amphistegina* sp. Beside foraminifers, very rare coralline algae and tubes of *Ditrupa* sp. occur. Matrix rich in abundant bioclastic debris, mainly nummulitic, is commonly observed (Fig. 3C). The bioclasts are often fragmented and abraded. The orthophragminid tests in this facies display the average T/D (thickness/diameter) ratio of 0.4–0.5. The contact with the overlying *Discocyclina* rudstone is sharp (Fig. 3A).

The *Discocyclina* rudstone, up 2 m thick, is built almost exclusively of the macrospherical forms of *Discocyclina* (A/B ratio 21/1). The lower part of the rudstone is dominated by saddle-shaped *Discocyclina pratti* (Michelin); moreover, disc-shaped *Discocyclina sella* (D'Archiac) and *Discocyclina* sp. (Fig. 3D, E), as well as not numerous ovate-shaped *Asterocyclina* sp. and *Orbitoclypeus* sp. occur. The lower part of the rudstone contains *Discocyclina* tests with the average T/D ratio of 0.2–0.25. In its upper part, the orthophragminid tests become thinner and flattened, dominated by disc-shaped *Discocyclina sella* (D'Archiac), with single *Discocyclina augustae* Wejden and *Discocyclina radians* (D'Archiac), and less numerous saddle-shaped *Discocyclina* sp. (Fig. 3F, G). The upper part of

the rudstone contains *Discocyclina* tests with the average T/D ratio of up to 0.2. The tests are horizontally orientated, densely packed, commonly with stylolitic contacts, with rare signs of fragmentation or abrasion. In the upper part of the *Discocyclina* rudstone, the lack of abraded detritus is observed (Fig. 3F). The uppermost part of the *Discocyclina* rudstone contains glauconite grains, in some cases with relics of planktonic foraminifera.

DISCUSSION

Depositional environment

The *Nummulites-Discocyclina* bioclastic packstone comprises high-diversity LBF community with numerous spherical, ovate and massive tests of *Nummulites* and *Discocyclina*. Such a test morphology strongly reflects ecological and physical condition of relatively shallow photic-zone and high-energy regime. The observed moderate abrasion (outer wall partly missing and damaged), reworking and fragmentation of the tests suggest allochthonous biofabric of *Nummulites* and *Discocyclina* (Racey, 2001; Beavington-Penney, 2004; Beavington-Penney & Racey, 2004; Beavington-Penney *et al.*, 2006). In turn, micrite-rich fabric and diverse fauna assemblage of varied palaeoecological modes suggest redeposition from shallower parts of the ramp to the deeper setting (*cf.* Afzal *et al.*, 2011). All this evidence that the discussed *Nummulites-Discocyclina* bioclastic packstone displays features typical of deposition in the proximal mid-ramp setting dominated by intense redeposition processes.

The overlying *Discocyclina* rudstone is almost exclusively composed of *Discocyclina* tests with domination of megalospherical A-forms (the ratio A/B forms is 21/1). According to Aigner (1985), strong dominations of the

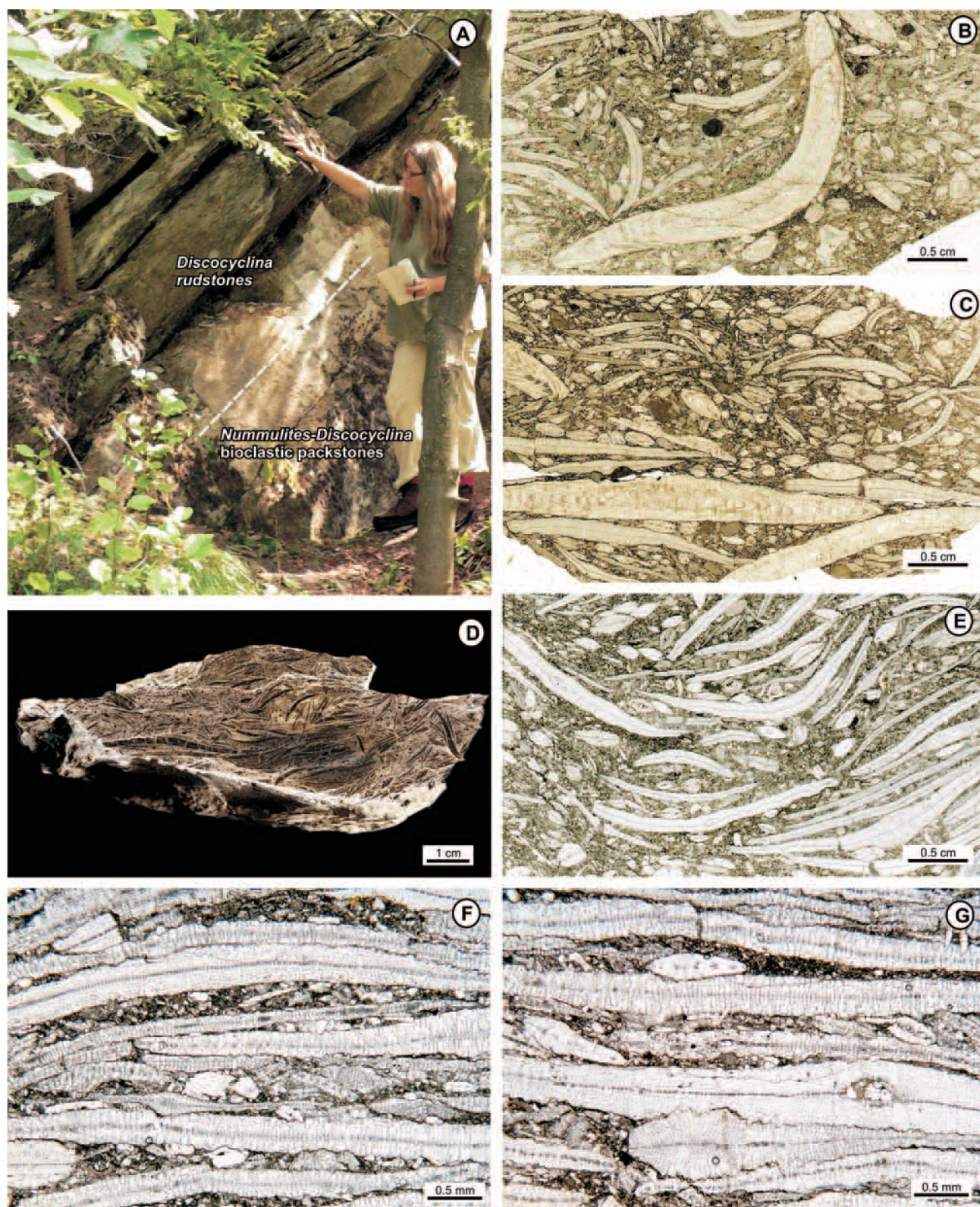


Fig. 3. *Discocyclina*-bearing facies, Bartonian, Pod Capkami Quarry section. **A.** Pod Capkami Quarry section – general view. The lower massive part of the section formed by *Nummulites-Discocyclina* bioclastic packstone; while the upper part is built up of distinctly bedded *Discocyclina* rudstone. **B.** *Nummulites-Discocyclina* bioclastic packstone composed of various small and spherical *Nummulites* sp. and saddle-shaped *Discocyclina* sp. as well as *Orbitoclypeus* sp., *Asterocyclina* sp., and *Discocyclina* sp., *Nummulites* cf. *maximus* (Orbigny); scan of the thin section. **C.** *Nummulites-Discocyclina* bioclastic packstone; scan of the thin section. **D.** *Discocyclina* rudstone general view; polished slab. **E.** *Discocyclina* rudstone – lower part of the facies. The rudstone, besides saddle-shaped *Discocyclina* sp. tests, is composed of numerous ovate-shaped *Orbitoclypeus* sp. and small, spherical *Nummulites* sp.; scan of the thin section. **F.** Disc-shaped *Discocyclina sella* (D'Archiac) tests horizontally orientated and densely packed, with stylolitic contacts; thin section. **G.** Disc-shaped *Discocyclina sella* (D'Archiac) tests horizontally orientated and densely packed, with stylolitic contacts; thin section

A-forms is typical of parautochthonous deposits. Hottinger (1997) regarded such an assemblage with dominance of megalospheric forms as an indicator of marginal depth range of the population. Low-diverse foraminifera community of *Discocyclina* rudstone facies is caused by strongly oligotrophic condition (Ćosović & Drobne, 1995; Racey, 2001; Ćosović *et al.*, 2004; Bassi, 2005; Afzal *et al.*, 2011).

The *Discocyclina* rudstone assemblage is parautochthonous, which is proved by test-supported fabric, scarcity of micrite and well preserved *Discocyclina* tests (*cf.* Aigner, 1985; Racey, 2001; Yordanova & Hohenegger, 2002). Analogous facies was described as deposited in distal mid-ramp and outer-ramp settings (Pappazoni, 1994; Racey, 2001; Afzal *et al.*, 2011). Probably, low degree of tests abrasion and scarce occurrence of micrite are an effect of intense winnowing, below the storm wave base (Aigner, 1982), which leads to concentrations of *Discocyclina* tests (Fig. 3F, G). Thus, the test-supported fabric seems to be an effect of winnowing and slower sedimentation rate (Aigner, 1982; Bassi, 2005).

Generally, transition from the highly-diverse LBF community dominated by *Nummulites* and *Discocyclina* to the low-diverse community dominated by *Discocyclina* reflects successive deepening of the depositional environment and lowering of energy regime. Thus, the *Discocyclina*-bearing facies marks progressive deepening from proximal mid-ramp setting to distal mid- and outer-ramp. It is additionally supported by occurrence of rare planktonic foraminifera in the uppermost part of *Discocyclina* rudstone.

Variation of orthophragminid test morphology

Along with the above discussed changes in the LBF composition, the changes of orthophragminid morphotypes is visible in the studied section. The vertical transition of orthophragminid morphotypes is clearly recorded up the studied section, whose lowermost part is dominated by ovate- and fusiform-shaped orthophragminids (*Discocyclina* sp., *Orbitoclypeus* sp., *Asterocyclina* sp.). Ovate and fusiform shape tests with thick wall reflect shallower environment with characteristic high energy and high light conditions (*e.g.*, Hohenegger, 2009).

The saddle-shaped tests of *Discocyclina* dominate in the upper part of *Nummulites-Discocyclina* packstone and in the lower part of *Discocyclina* rudstone. The saddle-shaped tests of *Discocyclina* have already been interpreted by Bieda (1963) who suggested that this morphology of tests is an adaptation to increase in the adherence capability of the test to plants. According to Olempska (1973), saddle-shaped tests are a physical adaptation to the irregularities of the substrate. However, based on the recent observations of undulate *Cycloclypeus*, it seems more probable that the saddle-shape of the tests is an adaptation to deeper euphotic zone. The saddle-shaped tests allow better absorption of sunlight, which strikes on the surface of the test at the different angle (Ferrandez-Cañadell & Serra-Kiel, 1992; Ferrandez-Cañadell, 1998; Beavington-Penney & Racey, 2004; Beavington-Penney *et al.*, 2006). Thus, this morphotype seems to be better adapted to a dim environment than to

shallow photic-zones where oval-shaped tests dominate (Hottinger, 1983; Hallock & Glenn, 1986; Hallock, 1999).

In the upper part of *Discocyclina* rudstone, flat, disc-shaped tests dominate. Such tests suggest low energy and very low light environment. Extremely flat disc-shaped tests, in the discussed case T/D ratio (up to 0.2), are characteristic for individuals living close to the extremes of their characteristic depth range. The tendency to flattening of disc-shaped tests and thinning of their walls is connected with requirements of algal endosymbionts of the LBF. Extremely flat disc-shaped tests of *Discocyclina* and their thin transparent hyaline walls allow light penetration into the interior of the tests (Hottinger, 1997; Renema, 2005; Hohenegger, 2009). Morphological resemblance between Eocene *Discocyclina* and recent *Cycloclypeus* suggests similar ecological conditions. *Cycloclypeus* species are observed in the deepest part of the photic zone, according to Pomar (2001) in oligophotic zone.

The above interpretation based on variation of orthophragminid morphotypes is consistent with the above discussed general trend of vertical facies variation being a record of deepening, lowering energy and gradual shadowing of the depositional milieu. Thus, orthophragminids seem to be a good and sensitive indicator of palaeoenvironmental conditions.

CONCLUSIONS

1. The *Nummulites-Discocyclina* bioclastic packstone represents proximal mid-ramp setting, whereas the *Discocyclina* rudstone typifies the distal mid-ramp and outer ramp.

2. The *Discocyclina* facies in the Pod Capkami Quarry section is a model example of LBF community response to transgression record. It is expressed in vertical change of orthophragminids morphotype from ovate through saddle- to disc-shaped tests.

3. *Discocyclina* test morphology is environmentally strongly controlled. Shallower settings are characterized by ovate-robust tests. Such test morphology is related to good illumination condition and higher energy regime. Flattened saddle-shaped or flattened disc-shaped tests are associated with deposition in dim setting and relatively lower energy regime.

4. Orthophragminids seem to be a good and sensitive indicator of palaeoenvironmental conditions.

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REFERENCES

- Afzal, J., Williams, M., Leng, M. J. & Aldridge, R. J., 2011. Dynamic response of the shallow marine benthic ecosystem to regional and pan-Tethyan environmental change at the Paleocene–Eocene boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 309: 141–160.
- Aigner, T., 1982. Event-stratification in Nummulite accumulations and in shell beds from the Eocene of Egypt. In: Einsele, G. & Seilacher A. (eds), *Cyclic and Event Stratigraphy*. Springer, Berlin: 248–262.
- Aigner, T., 1985. Biofabrics as dynamic indicators in nummulite accumulations. *Journal of Sedimentary Petrology*, 55: 131–134.
- Alexandrowicz, S. W. & Geroch, S., 1963. Association de petits Foraminifères dans l'Eocène de la Tatra. (In Polish, French summary). *Rocznik Polskiego Towarzystwa Geologicznego*, 33: 219–228.
- Bac-Moszaszwili, M., Burchart, J., Głazek, J., Iwanow, A., Jaroszewski, W., Kotański, Z., Lefeld, J., Mastella, L., Ozimkowski, W., Roniewicz, P., Skupiński, A. & Westwalewicz-Mogilska, E., 1979. *Geological map of the Polish Tatra Mountains 1:30 000*. (In Polish, English summary). Wydawnictwa Geologiczne, Warszawa.
- Bartholdy, J., Bellas, S. M., Čosović, V., Fuček, V. P. & Keupp, H., 1999. Process controlling Eocene mid-latitude larger foraminifera accumulations: modeling of the stratigraphic architecture of a fore-arc basin (Podhale Basin, Poland). *Geologica Carpathica*, 50: 435–448.
- Bartholdy, J., Bellas, S. M., Mertmann, D., Machaniec, E. & Manutsoğlu, E., 1995. Fazies-Entwicklung und Biostratigraphie einer Sequenz eoziäner Sedimente im Steinbruch Pod Capkami, Tatra Gebirge, Polen. *Berliner Geowissenschaftliche Abhandlungen*, 16: 409–425.
- Bassi, D., 2005. Larger foraminiferal and coralline algal facies in an Upper Eocene storm influenced, shallow-water carbonate platform (Colli Berici, north-eastern Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 226: 17–35.
- Beavington-Penney, S. J., 2004. Analysis of the effects of abrasion on the test of *Palaeonummulites venosus*: Implications for the origin of nummulithoclastic sediments. *Palaios*, 19: 143–155.
- Beavington-Penney, S. J. & Racey, A., 2004. Ecology of extant nummulitids and other larger benthic foraminifera: application in palaeoenvironmental analysis. *Earth-Science Reviews*, 67: 219–265.
- Beavington-Penney, S. J., Wright, V. P. & Racey, A., 2006. The Middle Eocene Seeb Formation of Oman; an investigation of a cyclicity, stratigraphic completeness and accumulation rates in shallow marine carbonate settings. *Journal of Sedimentary Research*, 76: 1137–1161.
- Bieda, F., 1963. Larger Foraminifera of the Tatra Eocene. (In Polish, English summary). *Prace Instytutu Geologicznego*, 37: 3–215.
- Čosović, V. & Drobne, K., 1995. Palaeoecological significance of morphology of orthophragminids from the Istrian Peninsula (Croatia and Slovenia). *Geobios*, 18: 93–99.
- Čosović, V., Drobne, K. & Moro, A., 2004. Palaeoenvironmental model of Eocene foraminiferal limestones of the Adriatic carbonate platform (Istrian Peninsula). *Facies*, 50: 61–75.
- Fermont, W. J. J., 1982. Discocyclinidae from Ein Avedat (Israel). *Utrecht Micropaleontological Bulletins*, 27: 1–173.
- Ferrandez-Cañadell, C., 1998. Morphostructure and paleobiology of Mesogea orthophragminids (Discocyclinidae and Orbitoclipeidae Foraminifera). *Acta Geologica Hispanica*, 31: 183–189.
- Ferrandez-Cañadell, C. & Serra-Kiel, J., 1992. Morphostructure and paleobiology of *Discocyclina* Gümbel, 1870. *Journal of Foraminiferal Research*, 22: 147–165.
- Geel, T., 2000. Recognition of stratigraphic sequences in carbonate platform and slope deposits: empirical models based on microfacies analysis of Paleogene deposits in of Cenozoic carbonate depositional facies. *Palaios*, 1: 55–64.
- Hallock, P., 1979. Trends in test shape with depth in large, symbiont-bearing Foraminifera. *Journal of Foraminiferal Research*, 9: 61–69.
- Hallock, P., 1985. Why are Larger Foraminifera large? *Paleobiology*, 11: 195–208.
- Hallock, P., 1999. Symbiont-bearing Foraminifera. In: Sen Gupta, B. K. (ed.), *Modern Foraminifera*. Kluwer, Dordrecht: 123–139.
- Hallock, P., Forward, L. B. & Hansen, H. J., 1986. Environmental influence of test shape in *Amphistegina*. *Journal of Foraminiferal Research*, 16: 224–231.
- Hallock, P. & Glenn, C. E., 1986. Larger Foraminifera: A tool for paleoenvironmental analysis of Cenozoic carbonate depositional facies. *Palaios*, 1: 55–64.
- Hallock, P. & Pomar, L., 2008. Cenozoic Evolution of Larger Benthic Foraminifera: Paleooceanographic Evidence for Changing Habitats. In: *Proceedings of the 11th International Coral Reef Symposium, Ft. Lauderdale, Florida, 7–11 July 2008*. Session number 1: 16–20.
- Hohenegger, J., 2004. Depth coenoclines and environmental considerations of Western Pacific larger foraminifera. *Journal of Foraminiferal Research*, 34: 9–33.
- Hohenegger, J., 2005. Estimation of environmental paleogradient values based on presence/absence data: a case study using benthic foraminifera for paleodepth estimation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 217: 115–130.
- Hohenegger, J., 2009. Functional shell geometry of symbiont-bearing benthic Foraminifera. *Galaxea, Journal of Coral Reef Studies*, 11: 81–89.
- Hohenegger, J. & Yordanova, E., 2001. Displacement of larger foraminifera at the western slope of Motobu Peninsula (Okinawa, Japan). *Palaios*, 16: 53–72.
- Hottinger, L., 1983. Processes determining the distribution of larger foraminifera in space and time. *Utrecht Micropaleontological Bulletins*, 30: 239–253.
- Hottinger, L., 1997. Shallow benthic foraminiferal assemblages as signals for depth of their deposition and their limitations. *Bulletin de la Société Géologique de France*, 168: 491–505.
- Jach, R., Machaniec, E., Uchman, A., in press. The trace fossil *Nummipera eocenica* from the Eocene nummulitic limestones, Tatra Mts., Poland: morphology and palaeoenvironmental implications. *Lethaia*.
- Jorry, J. S., Hasler, C. A. & Davaud, E., 2006. Hydrodynamic behavior of Nummulites: implications for depositional models. *Facies*, 52: 221–235.
- Kulka, A., 1985. Arni sedimentological model in the Tatra Eocene. *Kwartalnik Geologiczny*, 29: 31–64.
- Larsen, A. R., 1976. Studies of recent *Amphistegina*: taxonomy and some ecological aspects. *Israel Journal of Earth Sciences*, 25: 1–26.
- Larsen, A. R. & Drooger, C. W., 1977. Relative thickness of the test in *Amphistegina* species from the Gulf of Elat. *Utrecht Micropaleontological Bulletins*, 15: 225–239.
- Less, G., 1987. Paleontology and stratigraphy of the European Orthophragminae. *Geologica Hungarica, Series Palaeontologica*, 51: 1–373.
- Nebelsick, J. H., Rasser, M. W. & Bassi, D., 2005. Facies dynamics in Eocene to Oligocene circum alpine carbonates. *Facies*,

- 51: 197–216.
- Neumann, M., 1958. Revision des Orbitoidides du Cretacé et de l'Eocene en Aquitaine Occidentale. *Mémoires de la Société Géologique de France*, 38, 1–174.
- Olempska, E., 1973. The genus *Discocyclina* (Foraminiferida) from the Eocene of the Tatra Mts, Poland. *Acta Palaeontologica Polonica*, 18: 71–98.
- Olszewska, B., 2009. Small foraminifera of „Nummulitic Eocene” of the Tatra Mts. – stratigraphy and palaeoenvironment. (In Polish, English abstract). *Przegląd Geologiczny*, 57: 703–713.
- Olszewska, B. W. & Wieczorek, J., 1998. The Paleogene of the Podhale Basin (Polish Inner Carpathians) – micropaleontological perspective. *Przegląd Geologiczny*, 46: 721–728.
- Papazzoni, C. A., 1994. Macroforaminifers and paleoenvironments near the Middle-Upper Eocene boundary in the Mosano section (Berici Mts., Vicenza, northern Italy). In: Matteucci, R., Carboni, M. G. & Pignatti, J. S. (eds), *Studies on Ecology and Paleoecology of Benthic Communities. Bollettino della Società Paleontologica Italiana Special Volume*, 2: 203–212.
- Passendorfer, E., 1959. Eocene palaeogeography of the Tatra Island. (In Polish, English summary). *Biuletyn Instytutu Geologicznego*, 149: 259–271.
- Pomar, L., 2001. Types of carbonate platforms, a genetic approach. *Basin Research*, 13: 313–334.
- Racey, A., 2001. A review of Eocene nummulite accumulations: Structure, formation and reservoir potential. *Journal of Petroleum Geology*, 24: 79–100.
- Radomski, A., 1959. Podhale flysch sedimentation. (In Polish, English summary). *Acta Geologica Polonica*, 8: 335–409.
- Reiss, Z. & Hottinger, L., 1984. *The Gulf of Aqaba; Ecological Micropaleontology*. Springer, Berlin, 354 pp.
- Renema, W., 2005. Depth estimation using diameter-thickness ratios in larger benthic foraminifera. *Lethaia* 38: 137–141.
- Roniewicz, P., 1969. Sedimentation of the Nummulite Eocene in the Tatra. (In Polish, English summary). *Acta Geologica Polonica*, 19: 503–608.
- Serra-Kiel, J., Hottinger, L., Caus, E., Drobne, K., Ferrandez, C., Kumar Jauhri, A., Less, G., Pavlovec, R., Pignatti, J., Samso, J. M., Schaub, H., Sire, E., Strougo, A., Tambareau, Y., Tosquella, Y. & Zakrevskaya, E., 1998. Larger foraminiferal biostratigraphy of the Tethyan Paleocene and Eocene. *Bulletin de la Société Géologique de France*, 169: 281–299.
- Yordanova, E. K. & Hohenegger, J., 2002. Taphonomy of larger foraminifera: Relationships between living individuals and empty tests on flat reef slopes (Sesoko Island, Japan). *Facies*, 46: 169–203.